
PHYLOGENETIC ASSESSMENT *Mark A. HersHKovitz*² AND REVISED CIRCUMSCRIPTION OF *CISTANTHE* SPACH (PORTULACACEAE)¹

ABSTRACT

Reexamination of Carolin's cladistic analysis of Portulacaceae confirms that *Cistanthe* Spach should be segregated from *Calandrinia* Kunth and should include *Philippiamra* Kuntze. *Calyptridium* Nutt. in Torrey & A. Gray (including *Spraguea* Torrey) cannot be excluded from *Cistanthe* on phylogenetic grounds and is therefore recognized as a section therein. In all, *Cistanthe* includes 45–50 western American species in five sections, including *Cistanthe* sect. *Cistanthe*, *C.* sect. *Amarantoideae* (Reiche) Carolin ex HersHKovitz, *C. Calyptridium* (Nutt. in Torrey & A. Gray) HersHKovitz, *C.* sect. *Philippiamra* (Kuntze) HersHKovitz, and *C.* sect. *Strophium* (B. Mathew) HersHKovitz. The phylogenetic relationship of *Cistanthe* to other Portulacaceae indicated in Carolin's cladogram is, upon reanalysis, equivocal, and the relationships among the sections remain poorly understood. Biogeographic understanding of the taxa here included in *Cistanthe* has been obscured by earlier, unnatural, and sometimes erroneous classifications of these plants.

Cistanthe Spach is a putatively monophyletic genus of Portulacaceae comprising five sections and perhaps 45–50 western American species formerly classified in *Calyptridium* Nutt. in Torrey & A. Gray, *Philippiamra* Kuntze (\equiv *Silvaea* Philippi), *Spraguea* Torrey, five sections of *Calandrinia* Kunth, and one subgenus of *Lewisia* Pursh (see Table 1 for sectional key, citations, and synonymy). In the present paper, I describe the taxonomic history of *Cistanthe*, evidence for its naturalness as a genus, its relationship to other Portulacaceae, evidence on phylogenetic relationships among the species, and its biogeography.

TAXONOMIC HISTORY

Spach (1836) segregated the Chilean species *Calandrinia grandiflora* Lindley, *C. glauca* Schrader, *C. discolor* Schrader, and *C. speciosa* Lehm. into a new genus, which he named *Cistanthe*. Virtually all subsequent workers (e.g., Franz, 1908; Kelley, 1973; McNeill, 1974; Nyanyano,

1986, 1990; Pax & Hoffmann, 1934; Reiche, 1897, 1898) continued to recognize these species in *Calandrinia* sensu lato (see Carolin, 1987). *Calandrinia* in the broadest sense includes more than 100 species of western North America, western South America, and Australia (Carolin, 1987, in press; Kelley, 1973).

Reiche (1897, 1898), in a revision of Chilean Portulacaceae, recognized 12 sections of *Calandrinia* s.l., including *Calandrinia* sect. *Cistanthe*, which corresponded to Spach's (1836) generic circumscription of *Cistanthe*. Reiche's (1897, 1898) keys and descriptions make evident a close interrelationship among *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae* (collectively, *Cistanthe* sect. *Cistanthe*) based on the common presence of distinctive, resinous-appearing, black bract and sepal markings (Carolin, 1987) and often pubescent seeds (Kelley, 1973). Reiche did not propose a common category comprising these four sections, which differ primarily with respect to plant size and branching habit (Carolin,

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TABLE 1. Taxonomy of *Cistanthe* Spach. Provided below is a key to the sections of *Cistanthe*, along with full citations, synonymy, and distributions (see Hershkovitz, 1990a).

1a. Stigmas and capsule valves 3(–4); sepals herbaceous, marked or unmarked; petals usually 5 or more; seeds strophiolate or estrophiolate, pubescent or glabrous.	
2a. Sepals herbaceous, marked or unmarked; pedicels mostly ≥ 2 mm; seeds strophiolate, pubescent or glabrous; sinuous and ribbonlike veins present or absent; western North America and western South America.	
3a. Sepals marked with black etchings; petals 5(–8); seeds mostly pubescent; plants perennial or annual, rarely without cauline leaves; sinuous and ribbonlike veins rarely absent; western South America and southwestern North America.	<i>Cistanthe</i> sect. <i>Cistanthe</i>
3b. Sepals unmarked; petals (7–)8–9(–12); seeds glabrous; plants perennial with basal leaves only; sinuous and ribbonlike veins absent; Washington and British Columbia.	<i>Cistanthe</i> sect. <i>Strophium</i>
2b. Sepals membranous, unmarked; pedicels mostly ≤ 2 mm; seeds estrophiolate, glabrous; sinuous and ribbonlike veins present; western South America.	<i>Cistanthe</i> sect. <i>Amarantoideae</i>
1b. Stigmas 2 and capsule valves 2 or none; sepals usually membranous at least along margin, unmarked; petals 4 or fewer; seeds estrophiolate, glabrous.	
4a. Fruit dehiscent by two valves; sepals rarely nearly completely herbaceous; ovules mostly more than 1; North America.	<i>Cistanthe</i> sect. <i>Calyptidium</i>
4b. Fruit indehiscent or irregularly dehiscent; sepals membranous; ovule 1; South America.	<i>Cistanthe</i> sect. <i>Philippiamra</i>

Cistanthe Spach, Hist. Nat. Vég. 5: 229. 1836.

1. *Cistanthe* sect. *Cistanthe*. LECTOTYPE: *Calandrinia grandiflora* Lindley.
Calandrinia sect. *Cistanthe* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.
Calandrinia sect. *Arenariae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Calandrinia sect. *Andinae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Calandrinia sect. *Rosulatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Ca. 30 spp. from Chile, Argentina, and Peru; 2 spp. from California/Mexico.
2. *Cistanthe* sect. *Strophium* (B. Mathew) Hershkovitz, Phytologia 68: 268. 1990. *Lewisia* subg. *Strophium* B. Mathew, The Genus *Lewisia* 139. 1989. LECTOTYPE: *Calandrinia tweedyi* A. Gray

TABLE 1. Continued.

1 sp. from Washington and British Columbia.	
3. <i>Cistanthe</i> sect. <i>Amarantoideae</i> (Reiche) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. <i>Calandrinia</i> sect. <i>Amarantoideae</i> Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897. LECTOTYPE: <i>Calandrinia salsoioides</i> Barnéoud in Gay. Ca. 4 spp. from Chile, Argentina, and Peru; 1 sp. from California, Arizona, and Mexico.	
4. <i>Cistanthe</i> sect. <i>Calyptidium</i> (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990. <i>Calyptidium</i> Nutt. in Torrey & A. Gray, Fl. N. Amer. 1(2): 198. 1838. TYPE: <i>Calyptidium monandrum</i> Nutt. in Torrey & A. Gray. <i>Spraguea</i> Torrey, Pl. Frémont. Smithsonian Contr. Knowl. 6(2) [err., 5(1)]: 4. 1853. Ca. 8 spp. from western North America.	
5. <i>Cistanthe</i> sect. <i>Philippiamra</i> (Kuntze) Hershkovitz, Phytologia 68: 269. 1990. <i>Philippiamra</i> Kuntze, Revis. Gen. Pl. 1: 58. 1891. LECTOTYPE: <i>Silvaea celosioides</i> Philippi. <i>Silvaea</i> Philippi, Fl. Atacam. 22. 1860 (non <i>Silvaea</i> J. D. Hook. & Arn. ex Baillon, 1858). 2–4 spp. from Chile and Peru.	

1987; Reiche, 1897, 1898). Reiche (1897) noted the similarity between *Cistanthe* sects. *Amarantoideae* and *Philippiamra*, but he classified the former in *Calandrinia* sect. *Amarantoideae* and the latter in *Silvaea* (see Table 1).

Pax & Hoffmann (1934), in their taxonomic revision of Portulacaceae, classified *Cistanthe* sects. *Amarantoideae* and *Cistanthe* (as part of *Calandrinia* s.l.) in Calandrinieae–Calandrininae; *Cistanthe* sect. *Calyptidium* (as *Calyptidium* and *Spraguea*), in Calandrinieae–Calyptridiinae; and *Cistanthe* sect. *Philippiamra* (as *Philippiamra*) in an informal group described as intermediate between Portulacaceae and Basellaceae. The sections of *Cistanthe*, in their former generic assignments, were each taxonomically associated with other relatively distantly related members of Portulacaceae (Carolin, 1987). Thus, Calandrininae also included *Talinum* Adans., *Anacampseros* L., and other genera; Calyptridiinae included *Monocosmia* Fenzl [= *Calandrinia* sect. *Monocosmia* (Fenzl) Hershkovitz (Hershkovitz, 1990b, 1991b, in press a)]; and *Philippiamra* was associated with *Ceraria* Pearson & Stephens and *Portulacaria* Jacq. (Carolin, 1987; Pax & Hoffmann, 1934). As noted above, *Cistanthe* sect. *Strophium* was thought to belong in *Lewisia*, which Pax & Hoffmann placed in tribe Portulaceae along with *Portulaca* L.

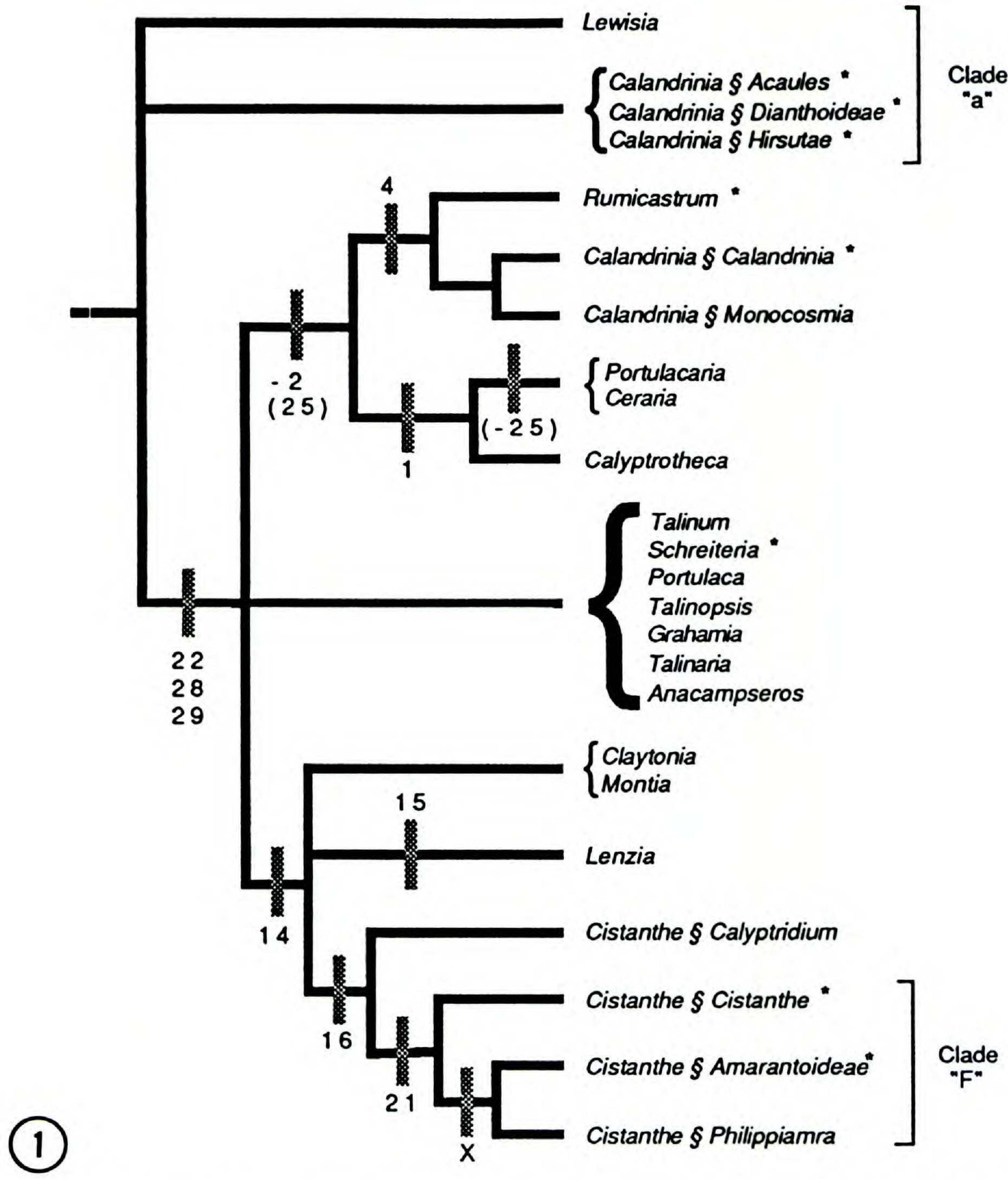


FIGURE 1. Simplified reproduction of Carolin's (1987: 402, fig. 7) most parsimonious cladogram of Portulacaceae, emphasizing the relationships among major clades and among members of *Cistanthe*. Taxa comprising traditional *Calandrinia* are starred. Only character state changes relevant to the present discussion of *Cistanthe* are shown. The numbered characters and "X" are Carolin's (see Table 2). All of the character state changes shown are regarded here as problematic (see text).

Kelley (1973), in his survey of seed and trichome morphology in the genus, maintained that *Calandrinia* s.l. was a natural assemblage. The traits Kelley cited as common to all the species (two sepals, three carpels, free-central placentation) are, cladistically, symplesiomorphic with many to all Portulacaceae. Kelley recognized the close interrelationship between *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae* (i.e., among members of *Cistanthe* sect. *Cistanthe*). Like Reiche (1897), Kelley remarked on the morphological similarities between *Cistanthe* sects. *Amarantoideae* and *Philippiamra*, but he did not recommend including these in a common genus.

McNeill's (1974) tribal classification of Portulacaceae is similar to that of Pax & Hoffmann (1934) in that the components of *Cistanthe* are placed in four different tribes.

Nyanyano (1986), in a revision of Portulacaceae, divided *Calandrinia* s.l. into three sections, but the sectional circumscriptions are anomalous and accord neither with those proposed elsewhere (cf. Carolin, 1987, in press; Kelley, 1973; Reiche, 1897, 1898), nor with the characterizations in his sectional key. Furthermore, many species of *Calandrinia* s.l., including all of the Australian element, are not accounted for in his treatment. In Nyanyano's three-section classification of *Calan-*

drinia s.l., members of *Cistanthe* sect. *Cistanthe* are included in two of the sections, while *Cistanthe* sect. *Amarantoideae* is included in the third. Each of Nyanyano's three sections includes taxa that, according to Carolin (1987) and Herskovitz (1990b, in press a), belong in different genera. Although Nyanyano (1986, 1990) recognized the relationship between *Cistanthe* sects. *Calyptridium* and *Philippiamra* (as distinct genera) and included both in tribe Calyptridieae, his circumscription of Calyptridieae is otherwise unnatural, and he went so far as to include *Monocosmia* in *Calyptridium* (cf. Herskovitz, in press a).

Carolin (1987), in his phylogenetic analysis of Portulacaceae, divided the existing sections of *Calandrinia* s.l. (see Cullen, 1953; von Poellnitz, 1934; Reiche, 1897, 1898) into 11 OTUs (excluding *Calandrinia* sect. *Partitae* von Poellnitz, which belongs in *Anacampseros*; see Carolin, 1987; Kelley, 1973). Carolin's OTU *Cistanthe* comprised *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae*. Perhaps the most significant finding of Carolin's analysis was that the OTUs of *Calandrinia* s.l. showed cladistic relationships with various genera throughout Portulacaceae, indicating that its erstwhile circumscriptions were unnatural (Fig. 1). The OTU *Cistanthe*, along with the OTUs *Amarantoideae* (= *Cistanthe* sect. *Amarantoideae*) and *Silvaea* (= *Cistanthe* sect. *Philippiamra*), formed clade "F" in Carolin's (1987, fig. 7) cladogram. Although lacking an unequivocal synapomorphy (see below), clade "F" corresponded with Carolin's (1987, in press) proposed generic circumscription of *Cistanthe*. Carolin (in press) proposed combining the OTUs *Amarantoideae* and *Silvaea* in a single section named for the former. In Carolin's (1987) analysis, clade "F" formed the sister group to the OTU *Calyptridium* (= *Cistanthe* sect. *Calyptridium*). Clade ["F" + *Calyptridium*] was diagnosed by one unique and nearly universally shared feature: the presence of unequal bracts associated with the inflorescence nodes (Fig. 2). Carolin (1987, in press) maintained *Calyptridium* as a distinct genus, however.

The present paper basically follows Carolin's (1987, in press) recommendation that *Cistanthe* be segregated from *Calandrinia* s.l., but the circumscription is modified to include *Calyptridium* and *Lewisia* subg. *Strophium* as distinct sections, and Carolin's OTUs *Amarantoideae* and *Silvaea* are each assigned to their own section (see Table 1).

PHYLOGENETIC ASSESSMENT OF *CISTANTHE*

Figures 1 and 3 depict the relationships among Portulacaceae as determined in Carolin's (1987, fig. 7) cladistic analysis and subjectively reanalyzed here. As discussed below, these figures emphasize evidence pertaining to the monophyly of *Cistanthe*, the relationship of the genus to other Portulacaceae, and relationships within the genus. The taxonomy in Figures 1 and 3 follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Herskovitz (1990a, b, 1991b, in press a). The numbered characters are defined in Table 2. Figure 1 depicts Carolin's consensus tree and shows the character state changes occurring between the root of the tree and the terminal OTUs of *Cistanthe*, as well as selected character state changes that are relevant to the present discussion but involve other branches of the tree. All of the indicated synapomorphies are regarded here as equivocal or unwarranted, as explained below. Figure 3 emphasizes possible phylogenetic relationships among the sections of *Cistanthe* as speculated here on the basis of the data in Table 3 and shows the relationships of *Calandrinia* sects. *Calandrinia* and *Monocosmia* I have proposed elsewhere (Herskovitz, 1990b, in press a). *Cistanthe* sect. *Strophium* is not shown in Figure 1 because Carolin was unaware of the relationship of this taxon to *Cistanthe* rather than *Lewisia* (Herskovitz, 1990b, in press b).

1. THE MONOPHYLY OF *CISTANTHE*

Although the monophyly of *Cistanthe* in the circumscription proposed here is evidenced by only a single synapomorphy (Figs. 1, 3), additional traits reinforce the close interrelationships between the sections. For example, leaves of *Cistanthe* generally have winged (if present) petioles, clasping leaf bases, festooned brochidodromous venation (if sufficiently broad to show this trait), a primary vein that becomes obsolete at the leaf apex, ribbonlike veins, sinuous veins, and predominantly brachyparacytic stomata (Herskovitz, 1990b, in press b, 1991c). The combination of these leaf traits is absent among other Portulacaceae, although their value in cladistically diagnosing the genus remains uncertain.

2. PHYLOGENETIC RELATIONSHIP OF *CISTANTHE* TO OTHER PORTULACACEAE

Subjective reanalysis of Carolin's (1987) data in light of additional evidence from leaf morpho-

logical studies (Hershkovitz, 1990b, in press b, in press c, in prep.) indicates that the western American members of Portulacaceae (Fig. 3; Carolin, 1987, fig. 8; Hershkovitz, 1990b, 1991a, c, in prep.), including *Cistanthe*, form a cohesive and possibly monophyletic group. The western American taxa share similar habit, leaf base, petiole, and stomatal morphology (Hershkovitz, 1991a, in prep.). The distinction between the western American group and the eastern American/African group of Portulacaceae with respect to these characters suggests that one or more of the characters may help cladistically diagnose either group. The Australian endemic *Rumicistrum* Ulbrich (cf. Fig. 3), however, is morphologically intermediate between these two groups (Hershkovitz, 1990b, in press a, in prep.). The precise relationships of *Cistanthe* to other western American taxa remain uncertain pending additional analysis.

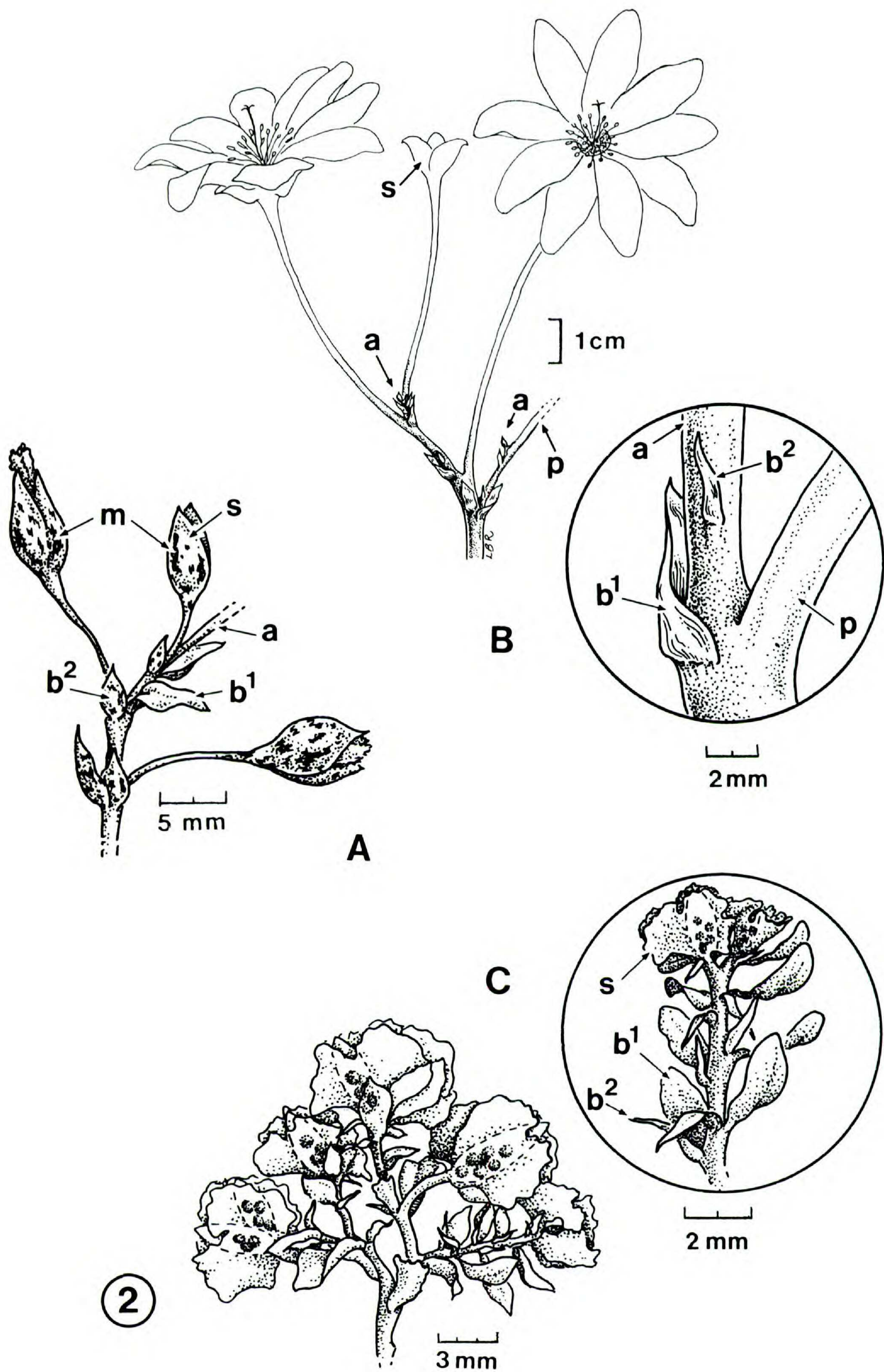
The phylogenetic relationships of *Cistanthe* indicated in Carolin's cladogram (Fig. 1) are more equivocal than they appear to be. The synapomorphies that diagnose Portulacaceae (including *Cistanthe*) minus Carolin's "secondary" clade "a" (not a clade in Carolin's consensus tree, Fig. 1) are problematic for several reasons. The synapomorphies are the change from more than five to five or fewer petals (character 22), and the two-step change from five or more to four to three or fewer stigmas (characters 28 and 29). Five petals and/or three stigmas characterize several species in each of the excluded OTUs, however (see Mathew, 1989, for *Lewisia*; and Reiche, 1898, for the pertinent sections of *Calandrinia*), and these characters show considerable reversal and rederivation in the clade diagnosed by low petal and stigma

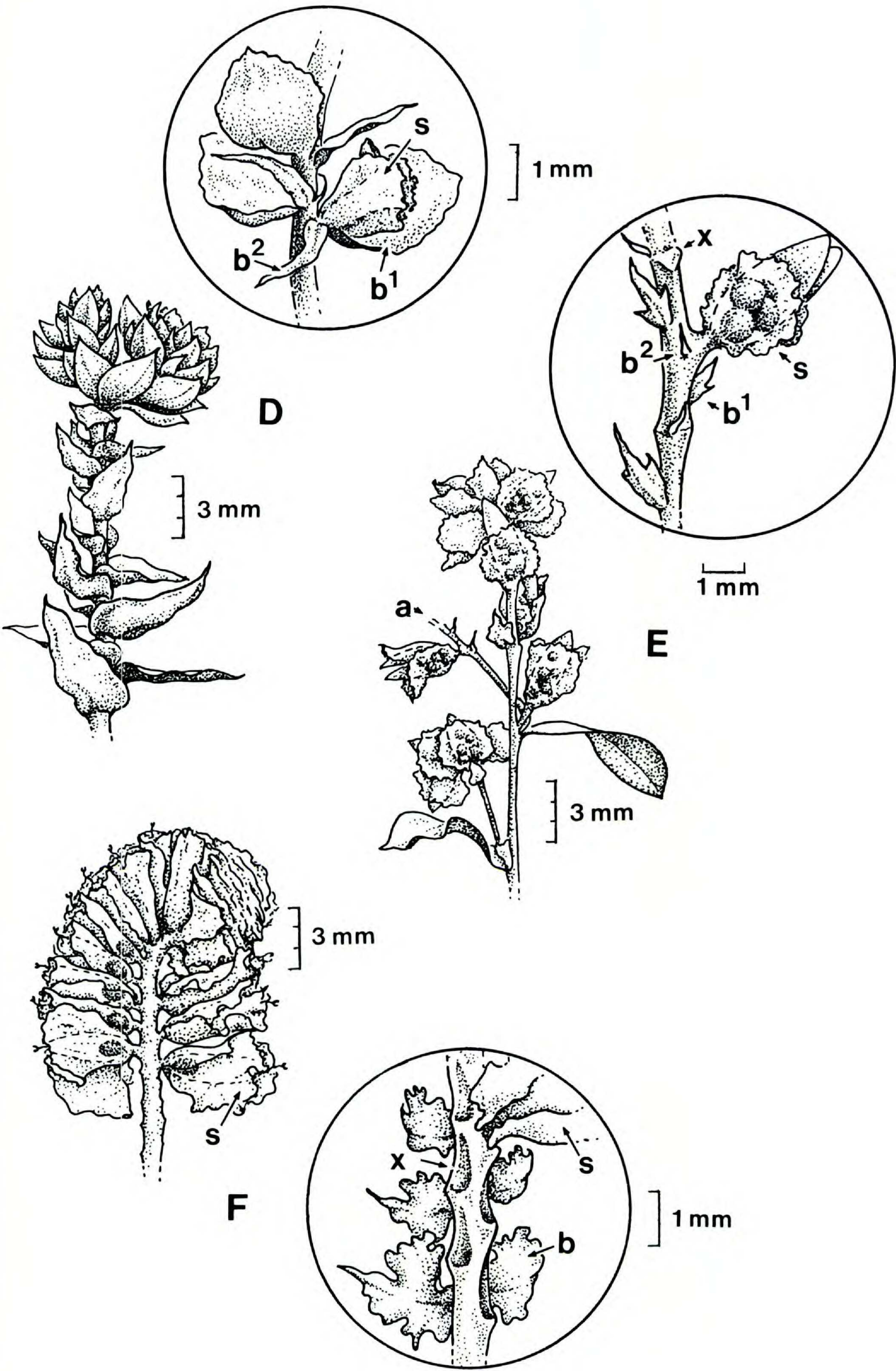
numbers (Carolin, 1987). The variability of these characters within and among the OTUs renders highly critical the accuracy of the character polarity assessment. Carolin based his polarity assessments for these characters in Portulacaceae (and, presumably, his assumptions on primitive states within OTUs) on the outgroup relationships proposed in Rodman et al.'s (1984) cladistic analysis of Centrospermae. In fact, based on that study, the polarities of these characters would be equivocal because one outgroup (Aizoaceae + Cactaceae) was scored for having high petal and stigma numbers, whereas the other (Basellaceae + Didieriaceae) has low petal and stigma numbers exclusively. This point is moot, however, because Rodman et al.'s (1984) character definitions and/or scores for floral characters and, for that matter, most aspects of their phylogenetic analysis have been heavily criticized (Levin, 1985; Bittrich, 1990; Bittrich & Hartmann, 1988; Hershkovitz, 1989; Rodman, 1990). Also, I have elsewhere (Hershkovitz, 1991a, in prep.) maintained that Cactaceae, Didieriaceae, and Basellaceae are each phylogenetically nested among Portulacaceae.

Carolin's (1987) treatment of the petal and stigma characters is problematic for other reasons as well. For example, it is not clear whether petals in Portulacaceae are homologous to the sepals or stamens of apetalous Centrospermae, to similar structures in other "petaloid" Centrospermae, or even to petals in the currently unknown outgroups of Centrospermae (see Cronquist, 1981, 1988; Levin, 1985; Rodman, 1985). Also, the change from five to three stigmas should not require two steps, as it does in Carolin's (1987) analysis.

In the absence of unequivocal outgroup rela-

FIGURE 2. Inflorescence bract morphology in *Cistanthe*. — A. *C. (Cistanthe) grandiflora* (Ford & Penalosa 497, MO). Terminal portion of inflorescence showing unequal bracts at the flowering nodes and bract and sepal markings. — B. *C. (Strophium) tweedyi* (Thompson 6463, US). Portion of inflorescence showing (inset) unequal bracts at the flowering node. The smaller bract is displaced apically on the continuing axis. (Modified from Hershkovitz, in press b.) — C. *C. (Amarantoideae) calycina* (Johnston 5313, US). Terminal portion of inflorescence showing (inset, with all but the uppermost flowers absent) unequal bracts associated with the flowering nodes. — D. *C. (Philippium) celosioides* (Zollner 7811, NA). Terminal portion of inflorescence showing (inset, with the upper two flowers absent) unequal bracts at the flowering nodes. — E. *C. (Calyptridium) parryi* var. *parryi* (Munz 5726, UC). Terminal portion of inflorescence showing (inset, with upper and lower flowers absent) unequal bracts associated with the flowering nodes. The smaller of the two associated inflorescence bracts is usually adjacent to the pedicel, while the larger bract occurs a short distance below. — F. *C. (Calyptridium) monosperma* (Johannsen 2394, UC). Terminal portion of inflorescence showing (inset, with all but the uppermost flower absent) single large bract associated with the swollen flowering nodes. The flowers are arranged in a two-ranked alternating pattern on the convex side of the coiled inflorescence branches, and the bracts are likewise arranged on the concave side. The inflorescence nodes are swollen, and the pedicels are inserted in shallow sockets. a, continuing axis; b, bract; b¹, larger of the pair of bracts associated with the node; b², smaller of the pair of bracts associated with the node; m, black bract/sepal markings; p, pedicel; s, sepal; x, scar from removed or abscised flower. (Drawings by Lesley Randall.)





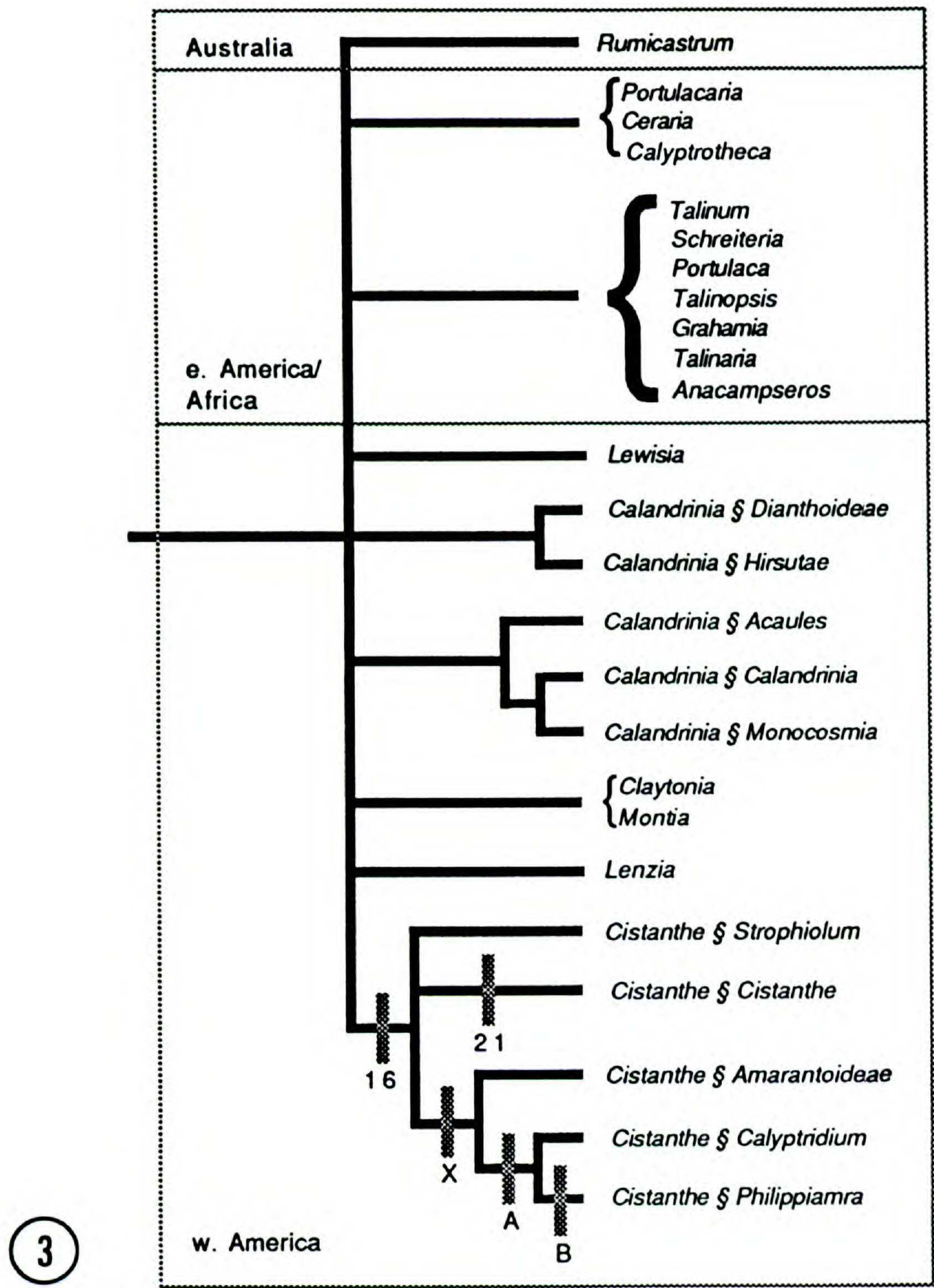


FIGURE 3. Revised cladogram of Portulacaceae derived by eliminating the questionable synapomorphies indicated in Figure 1 (see text). The numbered and lettered characters are defined in Table 2. The relationships shown for *Calandrinia* sects. *Calandrinia* and *Monocosmia* are after Hershkovitz (1990b, in press a), and the relationships shown among the members of *Cistanthe* are discussed in the present text. The boxes enclosing portions of the diagram circumscribe the regions of endemism or greatest endemism of the included taxa (Carolin, 1987; Hershkovitz, in press a, in prep.).

tionships for Portulacaceae, the evolutionary polarity of petal and stigma numbers for this family cannot be determined a priori, nor can primitive states be arbitrarily designated in those genera variable for these characters. In the context of Carolin's cladogram, therefore, the synapomorphies diagnosing the basal node must be regarded as unwarranted.

Because the basis for the exclusion of Carolin's

(1987) clade "a" from the remainder of Portulacaceae (Fig. 1) is questionable, the sole synapomorphy that diagnoses the clade (*Lenzia* Philippi + *Cistanthe* (in the present sense) + tribe Montieae Dumort.), the derivation of a monochasial inflorescence from "dichasia passing into monochasia" (character 14), also becomes problematic. Monochasia and/or solitary flowers occur in several members of clade "a." Dichasial inflorescence

TABLE 2. Characters referred to in Figures 1 and 3. The numbered characters and character "X" correspond to Carolin's (1987: 392, 412, appendix 3). The character states given first are those supposed by Carolin to be primitive. The polarities for characters 1, 2, and 4 are derived from Carolin's text because those indicated in his appendix appear erroneous. Some of Carolin's polarity determinations are discussed in the present text. Characters A and B are defined here; the state given first is considered primitive.

Char- acter no.	Character: primitive state vs. derived state
1	Growth form: not phanerophyte vs. phanero- phyte
2	Growth form: not suffruticose and/or passive chamaephyte vs. suffruticose and/or passive chamaephyte
4	Growth form: not therophyte vs. therophyte
14	Inflorescence: "dichasial passing into monocha- sia" vs. monochasial or solitary
15	Inflorescence: not solitary vs. solitary
16	Inflorescence bracts: equal vs. unequal
21	Sepal markings: absent vs. present
22	Petals: more than 5 vs. 5 or less
25	Pollen: trizonocolpate vs. panporate
28	Stigmas: 5 or more vs. less than 5
29	Stigmas: 4 or more vs. less than 4
31	Fruit: dehiscent vs. indehiscent
X	Inflorescence: open with long pedicels vs. con- densed with short pedicels
A	Carpel number: 3 or more vs. 2
B	Fruit: indurate vs. membranous

branching in *Lewisia* is restricted to species of *L.* sect. *Cotyledon* J. E. Hohn ex B. Mathew, and there is no strong evidence that section is otherwise primitive within the genus (Hershkovitz, 1990b, in press b; but see also Hohn, 1975); i.e., the dichasia might be secondarily derived. Reiche (1897) and Hershkovitz (1990b) reported that dichasial branching rarely occurs in *Cistanthe*, but this is questionable (Hershkovitz, in press b). Closer examination of herbarium specimens reveals that superficially dichasial branching results when the internodes are not elongated.

The scoring of inflorescence types in Carolin's (1987) analysis is problematic for other reasons as well. Because the primitive state could not be assessed by outgroup comparison, Carolin based his inflorescence character transformation series on "general principles," presuming that metaxytriads are primitive among Portulacaceae. I suspect that Carolin is correct in this regard; nevertheless, in his cladogram, the taxa scored for having metaxy-

TABLE 3. Character states in the sections of *Cistanthe*. The sections of *Cistanthe* are listed in the first row. The outgroups are inferred to be the remainder of Portulacaceae; the likely primitive character states, where known, are indicated. Parentheses denote rare character states.

Character	Outgroups	<i>Strophium</i>	<i>Cistanthe</i>	<i>Amarantoideae</i>	<i>Calyptridium</i>	<i>Philippium</i>
Inflorescence	open?	open	open (condensed)	condensed	condensed	condensed
Pedicel length (in flower)	> 2 mm?	> 2 mm	> 2 mm	usually < 2 mm	usually < 2 mm	< 2 mm
Bract/sepal markings	absent	absent	present	absent	absent	absent
Sepal texture (in flower)	herbaceous?	herbaceous	herbaceous	membranous	mostly membranous, at least along margin	membranous
Petal number	?	(7-)8-9(-12)	5(-8)	5	2-4	2-4
Carpel number	≥ 3	3	3(-4)	3	2	2
Capsule dehiscence	valvate	valvate	valvate	valvate	valvate	indehiscent
Capsule texture	indurate	indurate	indurate	indurate	indurate-membranous	membranous
Seed pubescence	absent	absent	present/absent	absent	absent	absent
Strophiole	?	present	present	absent	absent	absent
All basal leaves	?	yes	yes/no	no	yes/no	no
Sinuous leaf veins	?	no	yes (no)	yes	yes (no)	yes
Ribbonlike leaf veins	?	no	yes (no)	yes	yes (no)	yes

triads (*Portulacaria*, *Ceraria*, *Calypotrothea* Gilg, *Portulaca*) are nested among taxa having the supposedly more derived inflorescence types (see Carolin, 1987, fig. 7). Also, Carolin's transformation series requires that solitary flowers be derived from dichasia via monochasia; i.e., in two steps rather than one. This requirement appears to have influenced both the topology and number of steps in the most parsimonious cladogram. For example, except for the assumption that solitary flowers are derived from monochasia, *Lenzia* would not be included in the clade with *Cistanthe* and Montieae (see Fig. 1).

Other problems in Carolin's (1987) cladogram have an indirect effect on the assessment of the position of *Cistanthe* among Portulacaceae. For example, both synapomorphies (Fig. 1, characters 2, 25) supporting the clade comprised of *Rumic astrum*, *Calandrinia* sect. *Calandrinia* (\equiv *Calandrinia* sect. *Compressae* Reiche), *Calandrinia* sect. *Monocosmia*, *Portulacaria*, *Ceraria*, and *Calypotrothea* are problematic. The shared loss of the chamaephytic growth form (character 2) is essentially redundant with the subsequent derivations of the phanerophytic growth form (character 1) in *Calypotrothea*, *Ceraria*, and *Portulacaria*, and the therophytic growth form (character 4) in *Rumic astrum* and *Calandrinia*. Carolin treated different growth forms as different characters rather than different states of a single character. The derivation of pantoporate from tricolpate pollen (Fig. 1, character 25), which subsequently reverses in the *Portulacaria* + *Ceraria* clade, is equivocal: two independent derivations of pantoporate pollen would be equally parsimonious. In this case, two independent derivations seem more plausible, however, because there is no evidence elsewhere among angiosperms that tricolpate pollen can be rederived from pantoporate. Also, additional reanalyses of Carolin's (1987) cladogram and corroboration with leaf morphological evidence indicate that *Calandrinia* sects. *Calandrinia* and *Monocosmia* actually belong near *Calandrinia* sect. *Acaules* Reiche, rather than next to the *Rumic astrum* clade (Hershkovitz, 1990b, in press a, in press c).

Pending a thorough reanalysis of phylogenetic relationships among members of Portulacaceae and affiliated families, the position of *Cistanthe* will remain uncertain. If the problematic synapomorphies in Carolin's (1987) cladogram described above are disregarded, however, the basal polytomy shown in Figure 3 results. Figure 3 presumes that, in a formal reanalysis of Portulacaceae, *Cistanthe* would remain monophyletic. Preliminary reanalyses (D. Ford, unpublished; Hershkovitz, unpublished) in-

dicate that this will be the case. Figure 3 is not only highly unresolved, it is inherently inaccurate because of the probable paraphyly of Portulacaceae with respect to Basellaceae, Didieriaceae, Hectorellaceae, and possibly also Cactaceae (Hershkovitz, 1989, 1991a, unpublished). Also, two other members of Portulacaceae, *Talinella* Baillon and *Amphipetalum* Bacigalupo in Spichiger, were not included in Carolin's (1987) analysis and are not shown in Figures 1 and 3.

3. PHYLOGENETIC RELATIONSHIPS WITHIN *CISTANTHE*

The relationships among the sections of *Cistanthe* indicated in Figures 1 and 3 presume that all of the sections of *Cistanthe* are monophyletic. The monophyly of *Cistanthe* sect. *Cistanthe* is evidenced only by the universally shared presence of bract and sepal markings (Fig. 2A), although the trait is apparently lacking in aberrant specimens (Hershkovitz, 1991b). The possibility that this section is paraphyletic, therefore, should not be excluded, especially because this group otherwise shows variation for several of the characters listed in Table 3. *Cistanthe* sect. *Strophium* is monotypic, hence monophyletic. *Cistanthe* sect. *Philippiamra* appears to be monophyletic based on its fruit morphology. According to Table 3 and Figures 1 and 3, sects. *Amarantoideae* and *Calyptridium* lack an autapomorphy. A potential autapomorphy for sect. *Calyptridium* is the tetraploid condition found in all members of this section (see Hinton, 1975).

Based on their character states for carpel number, capsule dehiscence, and capsule texture, sects. *Amarantoideae*, *Cistanthe*, and *Strophium* appear to represent the primitive element of *Cistanthe* (see Fig. 3). Because the precise outgroup relationships of *Cistanthe* are not known, however, the data in Table 3 cannot corroborate an unequivocal hypothesis of relationship among these three sections. If the outgroups lack arils and have cauline leaves, sinuous and ribbonlike veins, and few petals (e.g., some *Rumic astrum* spp.), then sect. *Amarantoideae* likely represents the basalmost clade in the genus, and sect. *Strophium* would arise collaterally with sect. *Cistanthe*. If the outgroups possess the alternative states of these characters (e.g., some *Lewisia* spp.), then sect. *Strophium* would likely represent the basalmost taxon (see Hershkovitz, in press b)—a result that would have interesting biogeographic implications (see below). Most of the potential outgroups of *Cistanthe* (see Fig. 3), however, do not possess the

entire suite of traits that could unequivocally show either sect. *Amarantoideae* or sect. *Strophium* as the basal taxon in *Cistanthe*.

The difference between Carolin's (1987) and the present interpretation of the position of sect. *Calyptridium* can be accounted for, in part, by a problematic synapomorphy indicated in Carolin's cladogram (Fig. 1). Carolin's cladogram indicates that the absence of black bract and sepal markings (character 21) excludes sect. *Calyptridium* from the remainder of the genus. According to Carolin (1987), this trait is weakly evident in members of sect. *Amarantoideae*, but I have found no such evidence in the specimens I examined (see Hershkovitz, 1991b). (Carolin (in press), in his generic key to Portulacaceae, also reported markings in *Rumicistrum* and *Schreiteria* Carolin—I cannot confirm whether markings exist in these taxa.) Even if the markings occur in sect. *Amarantoideae*, however, their absence must be regarded as the primitive state unless this section is presumed to have arisen from within sect. *Cistanthe*. In any case, Carolin misscored sect. *Philippiamra* for having the markings. With this in mind, it should be clear from Figure 1 that sect. *Calyptridium* cannot be excluded from *Cistanthe* on the basis of this character.

The putatively derived position of sect. *Calyptridium* indicated in Figure 3 is based on its possession of a two-carpellate rather than three-carpellate gynoecium (shared with sect. *Philippiamra*), and a condensed rather than more open inflorescence (character "X" in Figs. 1, 3; not unique to sects. *Amarantoideae* and *Philippiamra*, contra Carolin, 1987). Other possibly significant characters (not indicated in Fig. 3) include fruit texture, sepal texture, and pollen morphology. The fruit texture in sect. *Calyptridium* is intermediate between the more indurate of sects. *Amarantoideae*, *Cistanthe*, and *Strophium*, and the more membranous of sect. *Philippiamra*. Like sects. *Amarantoideae* and *Philippiamra*, the sepals in sect. *Calyptridium* are usually at least partially membranous (Munz & Keck, 1973) rather than herbaceous (i.e., chlorophyllous). The last character is difficult to evaluate from herbarium specimens—even herbaceous bracts probably become more membranous with age and more so with herbarium processing. Finally, Nilsson (1967) noted a similarity in pollen morphology between sect. *Calyptridium* and sect. *Philippiamra*, although he did not extensively survey other members of *Cistanthe*.

In order to resolve phylogenetic relationships further among the sections of *Cistanthe*, it will be

necessary to resolve interspecific relationships within the sections. Only limited inferences can be made at present. For example, three species of sect. *Calyptridium* (*C. umbellata* (Torrey) Hershkovitz, *C. monosperma* (E. Greene) Hershkovitz, and *C. pulchella* (Eastwood) Hershkovitz) that collectively constituted *Spraguea* (Hinton, 1975) lack the smaller of the two bracts that characterize all other *Cistanthe* (Fig. 1E). The close relationship of these three species to the remainder of sect. *Calyptridium* seems beyond doubt (Hinton, 1975), so it seems reasonable to conclude that the former constitute a clade within the latter (and that the controversial genus *Spraguea* does, in fact, represent a natural grouping; cf. Hinton, 1975). *Cistanthe calycina* (Philippi) Carolin ex Hershkovitz and *C. ambigua* (S. Watson) Carolin ex Hershkovitz, both of sect. *Amarantoideae*, have a somewhat more open inflorescence (plesiomorphic?, see Table 3) than other species of the section. *Cistanthe ambigua*, the only North American species of sect. *Amarantoideae*, has especially long pedicels (plesiomorphic?, see Table 3) compared to the other species of this section (Kelley, 1973), but its leaf venation pattern is clearly derived (Hershkovitz, 1990b, 1991c). Thus, the classification of *C. ambigua* in sect. *Amarantoideae* deserves additional scrutiny. *Cistanthe* sect. *Cistanthe* is the most polymorphic and widely distributed section of *Cistanthe*, and while some apparently closely interrelated species groups can be identified (Hershkovitz, 1991b; Kelley, 1973; Reiche, 1898), the overall phylogenetic interrelationships remain obscure. The South American species of sect. *Cistanthe* are especially in need of revision (Hershkovitz, 1991b). Until this is accomplished, attempts to circumscribe taxonomic units for purposes of phylogenetic analysis may be futile. Phylogenetic resolution in sects. *Philippiamra* and *Strophium* is trivial. The former is monotypic, and while the number of species in the latter is not well established, the degree of polymorphism is clearly limited (Hershkovitz, 1991b).

BIOGEOGRAPHY OF *CISTANTHE*

Understanding of the biogeography of *Cistanthe* was obscured by pre-Carolin (1987) phylogenetic and biogeographic concepts of Portulacaceae, in which much of *Cistanthe* was included in *Calandrinia* s.l. The latter genus was regarded as basically western South American and Australian (Kelley, 1973; Raven & Axelrod, 1978). The only two North American species of *Cistanthe* formerly included in *Calandrinia* s.l., *C. ambigua* (Mojave

and Sonoran deserts) and *C. maritima* (Nutt. in Torrey & A. Gray) Carolin ex Hershkovitz (coastal California and Baja California), were presumed to have arrived from temperate South America via relatively recent (Quaternary?) long-distance and/or stepwise dispersal (Kelley, 1973; Raven & Axelrod, 1978). *Cistanthe* sect. *Philippiamra* was, presumably, conceived of as disjunct with the South African genera *Ceraria* and *Portulacaria* (see Carolin, 1987). *Cistanthe* sects. *Calyptridium* and *Strophium*, as *Calyptridium* and a species of *Lewisia*, respectively, are presumably among those North American Portulacaceae believed to have ultimately had a (temporally and phylogenetically non-specific) South American origin (see Raven & Axelrod, 1978).

The present synthesis of *Cistanthe* as illuminated by Carolin (1987) and emended here provides a previously unappreciated example of an amphitropical temperate disjunct taxon having considerable endemism in North and South America. Particularly critical to this biogeographic revelation is the determination that sect. *Calyptridium*, with eight species in North America, is not only related to other members of *Cistanthe* (Carolin, 1987; also implicit in Nilsson, 1967, and Nyanyano, 1986, 1990) but is also cladistically inextricable from the remainder of the genus (see above). Also significant is the recognition of the relationship of the Cascade-endemic *C. (Strophium) tweedyi* (A. Gray) Hershkovitz to *Cistanthe* (Hershkovitz, 1990b, in press b). Finally, the realization that *Cistanthe guadalupensis* (Dudley in D. Jordan) Carolin ex Hershkovitz (Guadalupe Island) belongs in *C. sect. Cistanthe* (Carolin, 1987; Hershkovitz, 1990a) rather than *Talinum* (Dudley, 1899) contributes an additional species to the North American element of *Cistanthe*. The misassignment of this species to *Talinum*, perpetuated in all pre-Carolin (1987) taxonomic treatments (e.g., Rydberg, 1932; Pax & Hoffmann, 1934; Wiggins, 1980), yielded a spurious interpretation of the distribution of *Talinum* (cf. Raven & Axelrod, 1978: 38).

Although the bulk (ca. 35 spp.) of *Cistanthe* remains South American, the degrees of morphological variation, ecological specialization, and geographical extent among the North American species are comparable. The diversity and distinctiveness of North American *Cistanthe* would not corroborate hypotheses that these species are either all recent immigrants from South America or descendants from a single common ancestral immigrant. *Cistanthe maritima* and *C. guadalupensis* may, in fact, represent relatively recent

arrivals—these species are morphologically very similar to South American members of sect. *Cistanthe*, and both have very limited distributions in open, hence invulnerable, coastal habitats. Because of its morphological distinctiveness, *C. ambigua* fails to fit the profile of a recent immigrant (see above). *Cistanthe* sects. *Calyptridium* and, especially, *Strophium* are also morphologically distinct from their North and South American counterparts. The possibility that sect. *Strophium* represents the sister group to the remainder of the genus is particularly significant, because it implies that *Cistanthe* was present at least as early in North America as, if not earlier than, in South America. Overall, no simple biogeographic scenario emerges to account for the diversity and distribution of North American *Cistanthe*.

LITERATURE CITED

- BITTRICH, V. 1990. Systematic studies in Aizoaceae. Mitt. Inst. Allg. Bot. Hamburg 23b: 491–507.
- & H. E. K. HARTMANN. 1988. The Aizoaceae—a new approach. J. Linn. Soc., Bot. 97: 239–254.
- CAROLIN, R. C. 1987. A review of the family Portulacaceae. Austral. J. Bot. 35: 384–412.
- . Portulacaceae. In K. Kubitzki (editor), Families and Genera of Vascular Plants, Volume 2. Springer Verlag, Heidelberg. (In press.)
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- . 1988. The Evolution and Classification of Flowering Plants, 2nd edition. New York Bot. Gard., Bronx, New York.
- CULLEN, D. C. A. S. DE. 1953. Las especies Argentinas del genero *Calandrinia*. Bol. Soc. Argent. Bot. 5: 1–29.
- DUDLEY, W. R. 1899. Report of the plants of Guadalupe Island. Pp. 280–283 in D. S. Jordan (editor), The Fur Seals and Fur-seal Islands of the Northern Pacific Ocean, Part 3. Gov. Printing Off., Washington, D.C.
- FRANZ, E. 1908. Beiträge zur Kenntnis Portulaceen und Basellaceen. Bot. Jahrb. Syst. (Beibl. 97) 42: 1–46.
- HERSHKOVITZ, M. A. 1989. Phylogenetic studies in Centrospermae: a brief appraisal. Taxon 38: 602–608.
- . 1990a. Nomenclatural changes in Portulacaceae. Phytologia 68: 267–270.
- . 1990b. Phylogenetic and Morphological Studies in Portulacaceae. Ph.D. Dissertation. University of California, Davis.
- . 1991a. More Centrospermae I: the portulacaceous alliance. Amer. J. Bot. 78(6, pt. 2): 191. [Abstract.]
- . 1991b. Taxonomic notes on *Cistanthe*, *Calandrinia*, and *Talinum* (Portulacaceae). Phytologia 70: 209–225.
- . 1991c. Leaf morphology of *Cistanthe* Spach. Ann. Missouri Bot. Gard. 78: 1022–1060.
- . In press a. A revised circumscription and sectional taxonomy of *Calandrinia* Kunth (Portulacaceae). Ann. Missouri Bot. Gard.

- . In press b. Leaf morphology and taxonomic analysis of *Cistanthe tweedyi* (nee *Lewisia tweedyi*; Portulacaceae). Syst. Bot.
- . In press c. Leaf morphology of *Calandrinia Kunth* (Portulacaceae). Ann. Missouri Bot. Gard.
- HINTON, W. F. 1975. Systematics of the *Calyptridium umbellatum* complex (Portulacaceae). Brittonia 27: 197–208.
- HOHN, J. E. 1975. Biosystematic Studies of the Genus *Lewisia*, section *Cotyledon* (Portulacaceae). Ph.D. Dissertation. University of Washington, Seattle, Washington.
- KELLEY, W. A. 1973. Pollen Morphology and Relationships in the Genus *Calandrinia* H.B.K. (Portulacaceae). M.S. Thesis. California State University, Northridge, California.
- LEVIN, G. A. 1985. Character analysis and cladistics: a response to Rodman et al. Syst. Bot. 10: 496–500.
- MATHEW, B. 1989. The Genus *Lewisia*. The Royal Botanic Gardens, Kew, England.
- MCNEILL, J. 1974. Synopsis of a revised classification of Portulacaceae. Taxon 23: 725–728.
- MUNZ, P. A. & D. D. KECK. 1973. A California Flora and Supplement, combined edition. Univ. California Press, Berkeley, California.
- NILSSON, Ö. 1967. Studies in *Montia* L. and *Claytonia* L. and allied genera. III. Pollen morphology. Grana Palynol. 7: 279–363.
- NYANYANO, B. L. 1986. Tribal and Generic Relationship and Classification of the Portulacaceae (Centrospermae). Ph.D. Dissertation. University of Reading, England.
- . 1990. Tribal and generic relationships in the Portulacaceae (Centrospermae). Feddes Repert. Beih. 101: 237–241.
- PAX, F. & K. HOFFMANN. 1934. Portulacaceae. Pp. 234–262 in A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 2. Auflage, Band 16c. Engelmann, Berlin.
- POELLNITZ, K. VON. 1934. Die *Calandrinia*-Arten Australiens. Feddes Repert. Beih. 35: 1–34.
- RAVEN, P. & D. A. AXELROD. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72: 1–134.
- REICHE, K. 1897. Zur Systematik der Chilenischen Arten der Gattung *Calandrinia*. Ber. Deutsch. Bot. Ges. 15: 493–503.
- . 1898. Flora de Chile, Volume 2. Univ. Chile, Santiago.
- RODMAN, J. E. 1985. Reply to Levin: “Honest effort was better than none at all.” Syst. Bot. 10: 500–503.
- . 1990. Centrospermae revisited, Part I. Taxon 39: 383–393.
- , M. K. OLIVER, R. R. NAKAMURA, J. U. MCCLAMMER & A. H. BLEDSOE. 1984. A taxonomic analysis and revised classification of Centrospermae. Syst. Bot. 9: 297–323.
- RYDBERG, P. A. 1932. Portulacaceae. Pp. 279–336 in R. Britton et al. (editors), North American Flora, Volume 21. New York Bot. Gard., Bronx, New York.
- SPACH, E. 1836. Histoire Naturelle des Végétaux: Phanérogames, Volume 5. Librairie encyclopédique de Roret, Paris.
- WIGGINS, I. L. 1980. Flora of Baja California. Stanford Univ. Press, Stanford, California.